

The University of Chicago

FLORAL MORPHOLOGY OF
CHRYSOETHAMNUS NAUSEOSUS
SPECIOSUS

A DISSERTATION SUBMITTED TO THE FACULTY
OF THE DIVISION OF THE BIOLOGICAL SCIENCES
IN CANDIDACY FOR THE DEGREE OF DOCTOR
OF PHILOSOPHY

DEPARTMENT OF BOTANY

1945

By
EDNA SNOW

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CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 567

EDNA SNOW

Introduction

Considerable work has been done on the morphology of the Compositae (2, 3, 4, 5, 6, 10, 13, 14, 15, 17, 18, 19, 20, 22, 23) but very little on the dominant composite plants of the west. HALL and CLEMENTS (11) have given attention to the taxonomy, origin, and relationship of the genera *Artemisia* and *Chrysothamnus*. DIETERT (6) made an extensive study of *Artemisia tridentata* Nutt. in

which he describes flower and seed development and development of leaf and stem. The present work was undertaken to extend the information on the floral development, gametogenesis, and vascular anatomy of one of the more abundant species of *Chrysothamnus*, *C. nauseosus speciosus* (Nutt.) Hall & Clements.

The genus *Chrysothamnus* is divided by HALL and CLEMENTS (11) into four sections, twelve species, and forty sub-

species. *C. nauseosus speciosus* is included in the section Nauseosi, the only one in which the twigs are densely pannose-tomentose. The group is characterized by a dense coating of long, weak hairs, more or less impregnated with a resinous substance. *C. nauseosus* exhibits the greatest variety of form.

C. nauseosus speciosus is a shrub 2-6 feet high, broad and rounded, usually blooming through September and October, sometimes even up to December. The rounded flower heads, usually consisting of five yellow disk flowers, are massed in such great numbers that the patches of color have given the plant the common name of goldenbush. It is also known in the Great Basin area as rabbitbrush, because rabbits utilize the thickets as a place of refuge.

This plant is found chiefly in the Great Basin region, although it occurs to some extent in all the western states. It occupies large areas of desert or semidesert country, frequently in pure stands, often along washes, on plains, and on mountain slopes. The species is deep-rooted and unfitted to compete successfully with the grasses in the surface soil. Under ecologically favorable conditions it is replaced by sagebrush or wheatgrass, but becomes re-established when such cover is broken by destructive grazing.

As a potentially important economic plant, it was investigated by HALL and CLEMENTS (11), who found rubber in the cortex and medullary rays of all twelve varieties examined. They estimated that the amount of rubber present averages about 2.83% but in individual plants may be as high as 6.57%. HALL and LONG (12) estimated that 150,000 tons of wild rubber are available in the roots and stems of this species, but the scattered and isolated location of the plants would make extraction and processing

almost prohibitive, except in case of extreme need.

MATERIAL AND METHOD.—The material used in this study was collected at Provo, Utah, beginning in March, 1943, and continuing each week until October 6 of the same year, and from August 18 through November 2, 1944.

Sectioning is difficult, since the bracts are covered with small clubshaped hairs which have considerable resinous substance within the cells. Resin ducts are regularly associated with the bundles and continue into the floral tube, although they do not occur with the bundles of the rest of the flower.

Formalin-acetic acid-alcohol killing and fixing agent was used exclusively because of its rapid penetration of the resinous tissues. The fixed buds were dehydrated by the tertiary butyl-alcohol method, imbedded in paraffin, sectioned, and stained in a modification of Flemming's triple stain. All sections were cut at 10 μ , with the exception of a few longisections for the study of megasporogenesis, which were cut at 12 or 15 μ . Cross and longisections were made of all the samples collected. All drawings, with the exception of figures 55 and 56, were made with a camera lucida.

Observations

FLORAL DEVELOPMENT

The leaf buds of *C. nauseosus speciosus* appear early in March, but the flower buds do not appear until August. Development of the buds and flowers is relatively rapid. There are no over-winter buds, and the whole process of bud formation up to fertilization occurs in a period of about 6 weeks. The collections of September 4 were the first in which the archesporial cell of the ovule had developed. At this time the microsporogenous cells were undergoing reductional divi-

sions. The pollen grains were mature about September 17, and the megagametophyte by October 6.

There are usually five disk flowers in a head, each in the axil of a bract. Ray flowers are absent. The appearance of the individual flowers is essentially acropetal, the lowest one first. The second differentiates very close to it, the third and fourth at about the same time, and the fifth somewhat later.

No evidence of flower primordia appeared until July 21. At that time there was a broadening of the stem tip, with no further change until about August 17, when the flower bud primordia began to appear. Each individual flower appears as a blunt protuberance in the axil of a bract on the broadened axis. Growth is more rapid in circumference than in length, thus broadening the primordium. Zonal growth occurs at the periphery of the protuberance. At the outer edge of this zonal portion the corolla differentiates first, followed by the stamens, then the pappus, and finally the carpels (figs. 4-7). The order of development of *Chrysothamnus* is similar to that of *Aster* and *Solidago* as reported by MARTIN (17), but differs from certain others as reported by COULTER and CHAMBERLAIN (5) and MERRELL (18), in which the order of differentiation is corolla, stamens, carpels, and finally pappus.

Large nectaries appear about the same time as the archesporial cell and develop almost simultaneously with the ovule. They are located at the base of the stamens adjacent to the style of the pistil.

The corolla lobes curve inward at an early stage. Their marginal cells interlock, bringing about a fusion of the lobes (fig. 12). The corolla remains sealed until forced open by elongation of the stamens (fig. 56), as also occurs in *Artemisia tridentata* Nutt. reported by DIETERT (6).

VASCULAR ANATOMY

The stele of the stem consists of five collateral bundles (fig. 13). At the tip of the stem five fibrovascular bundles are diverged from the stele (figs. 14, 15). Each of these is related to a single flower, of which there are five. At the base of each flower the vascular trace is similar in structure to the vascular bundle in the stem, of which it is a continuation.

Just above this level in each flower there diverge from the solid stele two vascular bundles on the side farthest away from the central axis of the stem (fig. 14). At a slightly higher level three more bundles (figs. 15, 55a-b) are diverged.

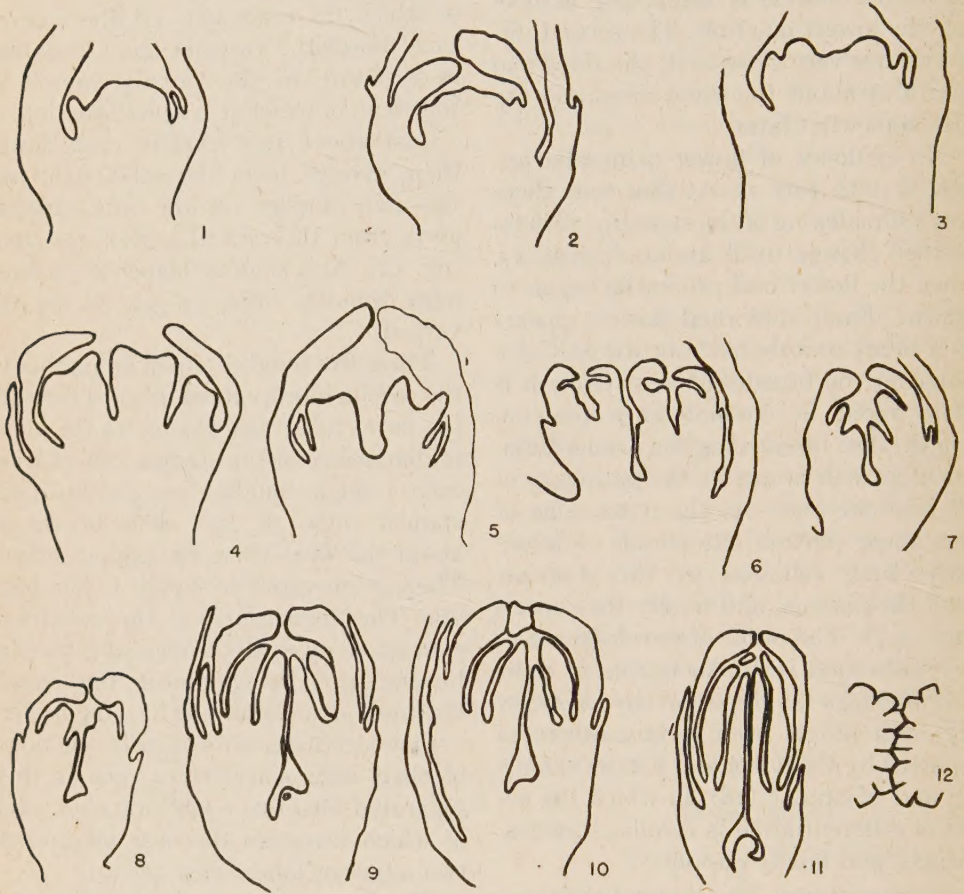
These five bundles, equal in number to the corolla lobes, extend upward through the floral tube (figs. 16, 29) to the point of divergence of the stamen, where from each a single bundle diverges into each stamen (figs. 28, 29). This occurs at about the level where the pappus arises. There is no vascular supply to the pappus. The main course of the bundles is continued upward through the corolla, but instead of being opposite to the middle lines of the lobes—as in some flowers—they alternate with them to the point of their divergence. Here each is then separated into two equal branches, each of which traverses the near margins of two adjacent lobes (figs. 31, 32).

The five major vascular bundles may be numbered in a clockwise direction, number 2 being opposite the main axis of the stem. Numbers 4 and 5 diverged first from the central stele; the other three somewhat higher.

A single bundle supplies the ovule. This is a continuation of two bundles which arise as divergences from numbers 1 and 3 of the three major bundles just described. They are distinct in the funiculus but extend as a single bundle

through the raphe and curve over the chalaza of the very large ovule, extending down the single integument. The two stylar bundles diverge from bundles 2 and 5 just above the top of the ovule, the former at a slightly lower level than the

the corolla was given by BROWN (1). *Chrysothamnus* is similar to the description given by him. The corolla of the primitive Compositae has a vascular supply of fifteen bundles—ten lateral, and five median (14, 15). The median vein of



FIGS. 1-12.—Figs. 1-5, section of young flowering branch, showing beginning of heads. Figs. 6-10, early stages in development of flowers. Fig. 11, young flower showing relation of parts at archesporial cell stage. Fig. 12, portion of two corolla lobes, showing interlocking of marginal cells.

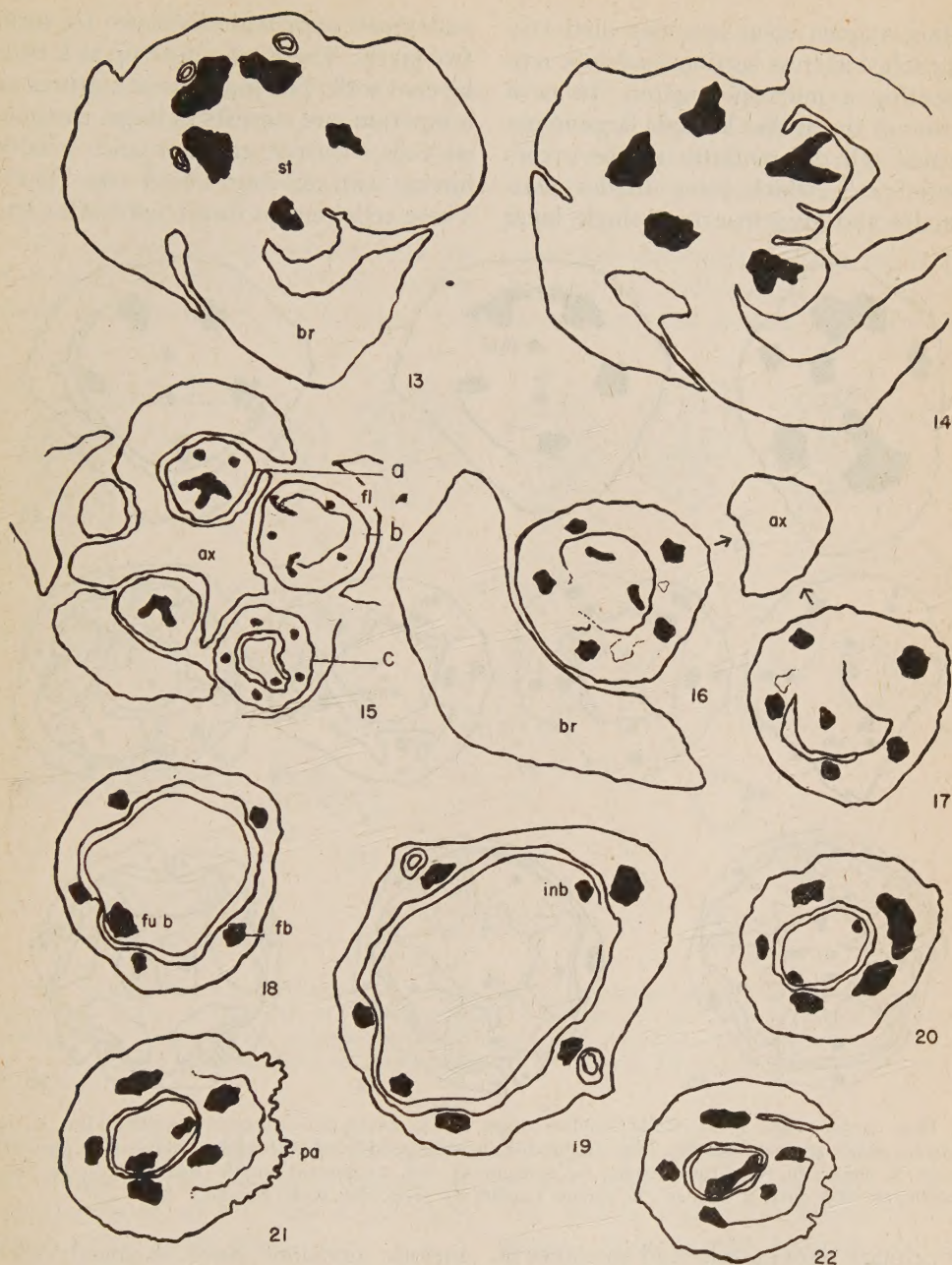
latter. These two bundles maintain their meristematic condition for a longer time than does the single bundle.

According to KOCH (14) the earliest mention of the venation of the corolla was by GREW in 1682, although the position of the veins was not discussed. The first clear description of the venation of

the petals is not present in *C. nauseosus speciosus*, there having been a reduction from this primitive condition to five bundles.

MICROSPOROGENESIS

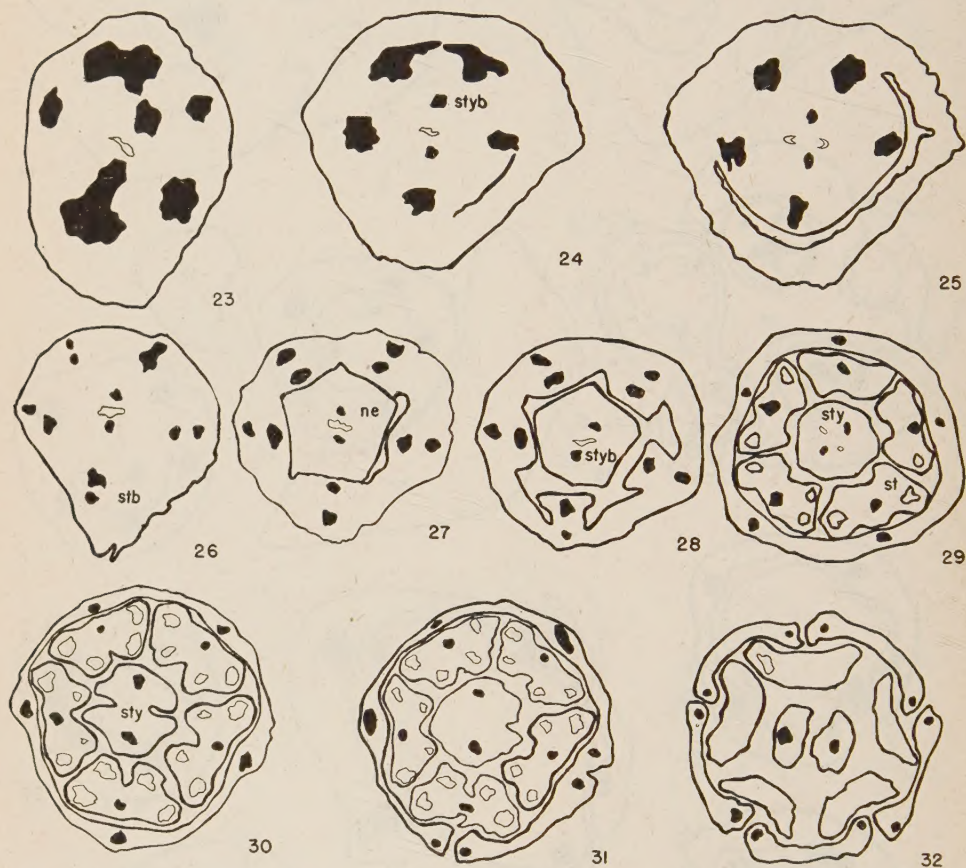
The five stamens diverge immediately above the divergence of the corolla. The



FIGS. 13-22.—Transections at different levels of flowering branch, tracing course of vascular system upward into individual flower: Figs. 13-15, tip of stem axis showing divergence into individual flowers. Fig. 16, individual flower, showing five major veins and bract. Figs. 17, 18, five bundles of floral tube and vein of funiculus. Figs. 19, 20, five bundles of floral tube and veins of funiculus and integument. Figs. 21, 22, section near top of ovule, showing curving of vein over chalaza; pappus being cut off.

young stamen soon becomes distinctly four-lobed in cross-section, each lobe representing a microsporangium. In each corner of the anther a single large hypodermal cell differentiates as the arche-sporial cell, which soon divides periclinally and gives rise to a single layer

undergoes periclinal divisions to form two layers. These later develop as a two-layered wall. The inner layer matures as a tapetum and consists of large, elongated cells, densely granular and usually having two or four nuclei (fig. 39A). These cells remain intact until after the



FIGS. 23-32.—Figs. 23-25, stylar bundles. Figs. 26-28, divergence of stamen bundles. Figs. 29, 30, stamen, stylar, and petal bundles. Figs. 31, 32, divergence of petal bundles to adjacent lobes. (ax, axis; brt, bract; fl, flower; fb, floral tube bundle; int, integument; inb, integument bundle; nec, nectary; pb, petal bundle; rd, resin duct; st, stamen; stb, stamen bundle; sty, style; styb, stylar bundle.)

of primary parietal cells and one layer of primary sporogenous cells. The primary sporogenous cell undergoes several successive anticlinal divisions, thus forming a group of four or five microspore mother cells.

Meanwhile the primary parietal cell

meiotic divisions have occurred; then they become digested, disintegrated, and absorbed by the developing spores. A similar condition was found in *Silphium* by MERRELL (18).

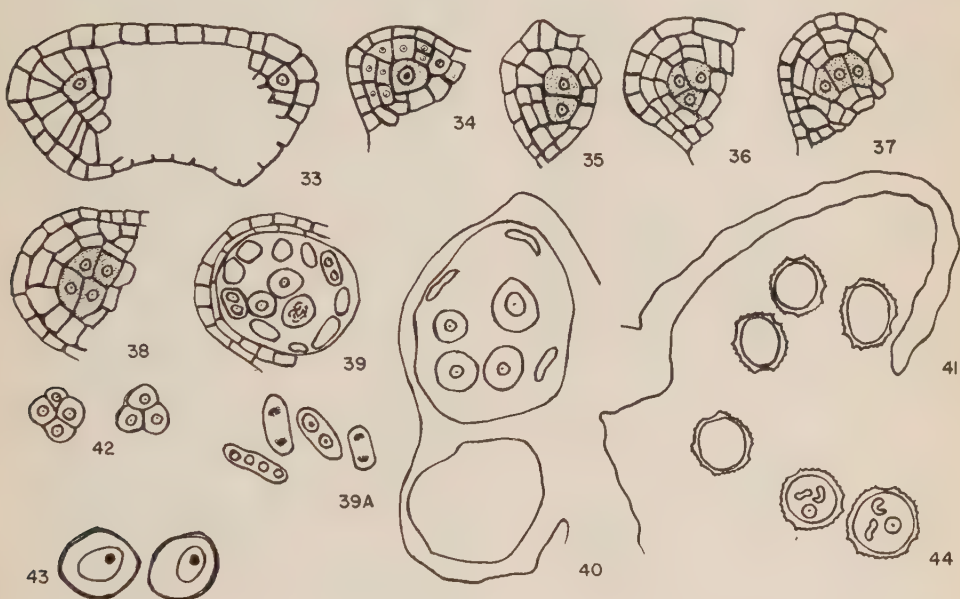
The microspore mother cells undergo meiosis (fig. 39), and the microspores

(fig. 43) are formed in tetrads (fig. 42). The tetrads split apart soon afterward, and after enlargement of the spore the nucleus divides to form a generative and a tube nucleus. The generative nucleus divides to form two spherical sperm nuclei which later elongate (fig. 44).

The mature microgametophyte in the anther is essentially spherical, having three furrows, and has a spinous wall

into the ovule instead of ending abruptly just below the edge of the funiculus. MERRELL states, "Whatever may be the condition in other Compositae, the ovule of *Silphium* as shown by its origin and its bundle relations is the termination of the floral axis, that is, the ovule is cauline."

Within the nucellar tissue the single hypodermal archesporial cell appears rather early and is easily recognized by



FIGS. 33-44.—Stages in development of anther: Figs. 33-38, sporogenous cells, primary parietal and tapetal layers. Fig. 39, pollen sac at microspore mother cell stage. Fig. 39A, cells of inner tapetal layer, showing two or four nuclei. Fig. 40, pollen sacs at microspore stage. Fig. 41, one-half mature anther, showing one pollen sac. Fig. 42, microspores, tetrad stage. Fig. 43, microspores. Fig. 44, microgametophyte at time of shedding.

(fig. 44). At this stage the sperm nuclei are elongated, are slightly crescent- to spindle-shaped, and lie free in the cytoplasm of the pollen grain.

MEGASPOROGENESIS

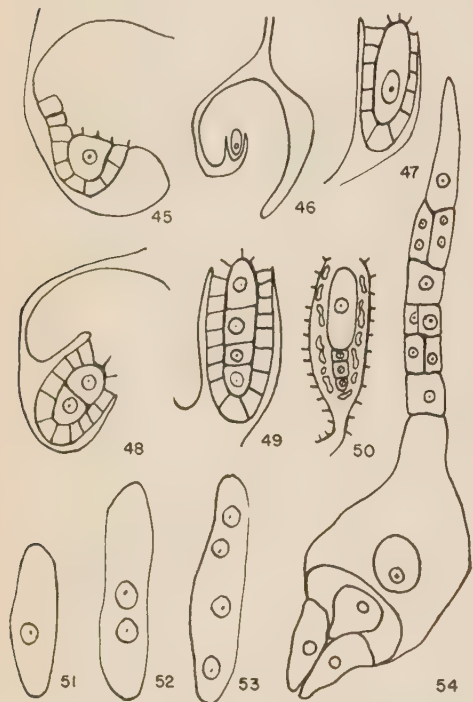
The nucellus arises from the placenta at the tip of the axis and appears to be cauline. In the ray flower of *Silphium* (18) the axial bundle extends directly

its large size, granular appearance, and greater affinity for stains (figs. 45-47). The archesporial cell enlarges rapidly without dividing and becomes directly the megaspore mother cell. The elongated spore is covered by a single layer of nucellus. It follows the usual pattern of meiosis, forming a linear tetrad (figs. 48, 49). Three megaspores, usually those nearest the micropylar end, disintegrate

(fig. 50). The remaining one increases rapidly in size, as does the ovule, which soon fills the ovary cavity (fig. 51).

The functional megaspore undergoes three successive divisions (figs. 51-54), as has been reported previously for other Compositae (4, 5, 6, 14), forming at first a gametophyte of the eight-nucleate type. Wall formation occurs, dividing it into

None of the material examined showed fusion of the polar nuclei, which came to rest near the egg cell, but it apparently occurred early. The egg cell is pear-shaped, attenuated toward the micropylar end. The synergids, which are in close contact with the egg, are rather slender, with attenuated ends which extend into the micropyle. As already stated, the antipodal cells often divide, so that a variable number is formed. These differ in size and arrangement. Megagametophytes having six to ten antipodal cells were found, and some of these cells had more than one nucleus (fig. 55). The antipodals are arranged in a more or less linear row, although in several cases two cells lie side by side. Often such cells have been cut off in planes at right angles to each other. The antipodal cell farthest from the micropyle is usually the largest. It elongates rapidly, often occupying about one-third of the space of the antipodal tissue. These results agree closely with those of CHAMBERLAIN (2) and OPPERMAN (19), but are in contrast with those of MARTIN (17), who found no walls for these cells, and not more than four antipodal cells, and never in a single longitudinal row. The antipodal tissue persists very late in the development of the embryo.



FIGS. 45-54.—Stages in development of megagametophyte: Fig. 45, archesporial cell stage. Figs. 46-49, development of megaspores. Fig. 50, disintegrating megaspores (high power). Fig. 51, functional megaspore. Figs. 52, 53, development of megagametophyte. Fig. 54, mature megagametophyte showing synergids, egg, polar nucleus, and nine antipodal cells.

seven distinct cells. Subsequent divisions of the antipodals occur. The mature megagametophyte occupies about one-half of the entire length of the ovule. The lower two-thirds of the sac is narrow and elongated, but the central region of the upper one-third increases in breadth.

GUIGNARD (8, 9) was one of the first to describe the increased development of the antipodals. He found them persisting and increasing in number up to ten uninucleate cells in *Conyza ambigua*. COULTER and CHAMBERLAIN (5) described as a common feature of the Compositae the enlargement of the distal antipodal cell and its penetration into the chalazal tissue. The nucellar cells adjacent to the antipodals are elongated and loosely connected. The antipodal cells are equal to—or exceed—the rest of the megagametophyte in length.

The nucellar tissue surrounding the two-thirds of the gametophyte nearest the micropyle begins disintegration almost simultaneously with that of the three nonfunctional megaspores, and few of its cells remain when the four-nucleate

The cells of the integument are narrowly columnar, compact, densely granular, stain darker, resemble a secondary nutritive layer, and form the "epithelial" layer characteristic of the Compositae as described by HOWE (13).

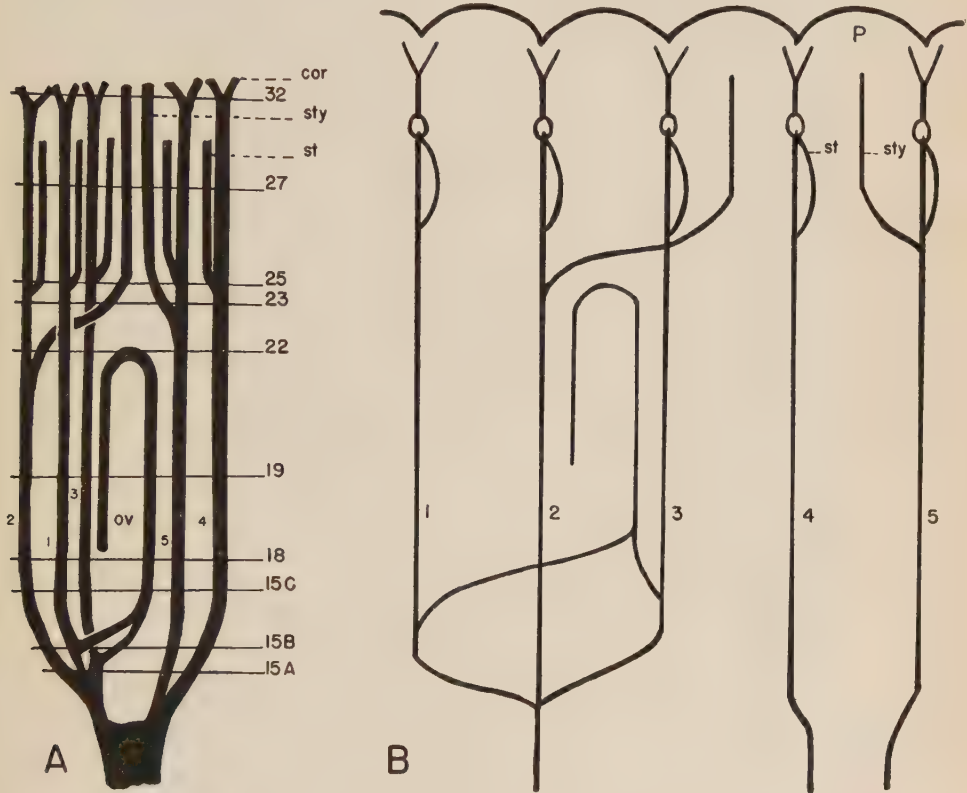


FIG. 55.—Diagram showing *A*, vascular anatomy of flower in longsection in three dimensions; *B*, same, in two dimensions.

stage of the megagametophyte is reached. When the megagametophyte is mature this nucellar tissue has disappeared. Following the disintegration of the nucellar tissue, one or two inner layers of cells of the integument closely surround and are in contact with the megagametophyte, except its antipodal portion—which projects into the tissue of the ovule near the chalazal region. This tissue becomes digested and absorbed by the gametophyte.

Discussion

The development of the flowers and the vascular anatomy of *Chrysanthamnus nauseosus speciosus* extends, and agrees somewhat with, the observations made by SMALL (22), CHAMBERLAIN (2, 3), MARTIN (17), KOCH (14, 15), MERRELL (18), OPPERMAN (19), BROWN (1), WARMKE (23), and GUSTAFSSON (10). In order of floral development it is like that of *Silphium*, in which the pappus appears

before the pistil, but unlike *Aster*, *Solidago*, and *Erigeron*, in which the pistil is the last structure to differentiate.

KOCH (14) describes the vascular system of the composite flower and divides it into four types. The fourth or discoid type which she describes is typical of *C. nauseosus speciosus*, and according to her it is the advanced type. In this type

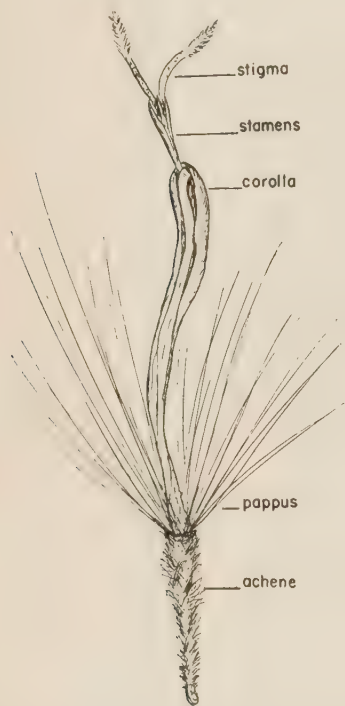


FIG. 56.—Old flower just prior to loss of corolla, stamens, and stigma.

there is an absence of midveins in the corolla lobes of the tubular flower. The presence of veins bordering the margins of the lobes is explained on the basis of the fusion of the lateral bundles of primitive Composites, and the loss of the median bundle. The five fused lateral bundles of the floral tube divide at the sinuses and border the corresponding lobes.

BROWN (1) describes this condition

and states that the Compositae agree in two points: "1. Valvular aestivation, or the margins of segments dehiscing like capsule valves. This may be found in other families. 2. The nerves of the corolla are equal to the lobes, but instead of being opposite and passing through their axes as in other plants, they alternate with them, each divides into two equal branches at the top of the tube."

The absence of pith in the stele as it diverges into the individual flowers is rather an unusual condition. So far as the writer is aware, this feature is not mentioned in the literature on the Compositae.

The styler bundles, diverging at slightly different levels from bundles 2 and then 5 (fig. 55A-B), bear out the work of SMALL (22). He states, "BROWN gives the orientation of the styler bundles correctly as antero-posterior and the ovarial bundles as lateral."

The vascular anatomy of a plant is especially important in explaining epigyny. The nature of the floral tube has been described by WILSON and JUST (24), and also by EAMES as reported by DOUGLAS (7). They state that there is abundant proof from the course of the bundles that the inferior ovary represents adnation in its extreme form. The vascular anatomy of *C. nauseosus speciosus* shows that the floral tube is not an invaginated axis but may be composed of undiverged basal parts of the flower. Certainly there is in *Chrysothamnus*, as well as in other Compositae, considerable zonal growth of all parts up to the top of the ovary (figs. 9, 10), and of the petals and stamen for a considerable distance above that level (fig. 11).

There seems to be general agreement that the Compositae are characterized in general by having male gametes existing as naked nuclei in the pollen grain,

elongated and curved, or irregular in shape (PODDUBNAJA [20] as reported by DIETERT [6]).

One notable feature in *Chrysothamnus* is the relatively extreme size of the ovule. It grows rapidly after the archesporial cell stage. A representative set of measurements showed the gametophyte to be about 1.4 mm. and the ovule about 3 mm. in length, the latter equaling about one-fourth the full length of the flower. In my material no ovules were found with more than a single archesporial cell.

The antipodal cells vary in number, size, and position, as well as in number of nuclei. The usual number of three antipodals was not seen in this species. Discussions of the number and character of the antipodal cells in the Compositae have been given by COULTER and CHAMBERLAIN (5), SMALL (22), and SCHNARF (21). The enlargement and extension into the chalazal tissue is common and corresponds with the description of *Artemisia* reported by DIETERT (6). Most investigators agree that the haustorial type of antipodals is concerned with the nutrition of the megagametophyte and that they aid either in digestion, or in conduction (or both) of substances to the gametophyte (8, 16, 20).

At the time the megagametophyte is developing, disintegration of some of the cells of the ovule occurs. These cells lie immediately interior to the epidermis of the ovule, principally in the chalazal region. The epidermis of the ovule remains intact and becomes thickened at the time the megagametophyte is mature, but the walls of the two layers of cells interior to it have been broken down. This seems to be a common occurrence in all the sections studied, but no mention of this disintegration has been found in the literature.

Summary

1. *Chrysothamnus nauseosus speciosus* (Nutt.) Hall & Clements is a potentially important economic shrub of western United States. It is 2-6 feet high, and is a subclimax dominant of the sagebrush-wheatgrass association.

2. It blossoms through September and October. The yellow flower heads are rounded, usually consisting of five disk flowers, with no ray flowers present.

3. The flower bud primordia appear during the latter part of August, and fertilization occurs the early part of October. The floral organs develop in the sequence: corolla, stamens, pappus, and pistil.

4. The marginal cells of the corolla lobes curve inward at an early stage, interlock, and bring about fusion of the lobes. Later the elongation of the stamens forces the flower open.

5. The fibrovascular bundles are equal in number to the corolla lobes but are alternate with their median lines rather than opposite. The styler bundles are antero-posterior, and the ovule bundle is lateral.

6. The mature microgametophyte at the time of shedding has three nuclei, a tube nucleus, and two elongated naked sperms.

7. A single archesporial cell was found in each ovule. It gives rise to four megaspores. The chalazal megaspore is the functional one.

8. The nucellus surrounding the mature megaspore mother cell and the four spores consists of one layer of cells. There is a single massive integument and a single large ovule. The inner layer of the integument is in contact with the megagametophyte and appears tapetal in nature.

9. The mature megagametophyte con-

sists of two synergids, an egg cell, two polar nuclei which fuse early, and a variable number of antipodals which show much diversity in their size, number, and arrangement, but are mainly linear. The number of antipodal cells varies from six to ten, each having from one to several nuclei. The cells are persistent and usually become haustorial in nature, penetrating the chalazal region and causing dis-

integration of the cells surrounding the region.

The writer acknowledges with sincere thanks the advice and help given by members of the Department of Botany of the University of Chicago during the course of this investigation.

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LITERATURE CITED

1. BROWN, ROBERT, Some observations on the natural family of plants called Compositae. Trans. Linn. Soc. 12:76-142. 1818.
2. CHAMBERLAIN, C. J., The embryo sac of *Aster novae-angleae*. BOT. GAZ. 20:205-213. 1895.
3. ———, The embryo sac of *Aster* and *Solidago*. BOT. GAZ. 65:571-572. 1918.
4. COULTER, J. M., Development of a dandelion flower. Amer. Nat. 49:609. 1915.
5. COULTER, J. M., and CHAMBERLAIN, C. J., Morphology of angiosperms. Macmillan Co. 1903.
6. DIETERT, R. A., The morphology of *Artemisia tridentata* Nutt. Lloydia 1:3-74. 1938.
7. DOUGLAS, GERTRUDE E., The inferior ovary. Bot. Rev. 10:125-187. 1944.
8. GUIGNARD, L., Sur le rôle des antipodes. Bull. Soc. Bot. de France 1881:197-202. 1881.
9. ———, Recherches sur le sac embryonnaire des Phanérogames Angiosperms. Ann. Sci. Nat. Bot. VI 13:136-199. 1882.
10. GUSTAFSSON, ÅKE, Über der embryosackmutterzelle bei *Taraxacum*. Bot. Notis. 1933:531-534. 1933.
11. HALL, H. M., and CLEMENTS, F. E., The phylogenetic method in taxonomy. The North American species of *Artemisia*, *Chrysothamnus*, and *Atriplex*. Carnegie Inst. Wash. Publ. 326. 1923.
12. HALL, H. M., and LONG, F. E., Rubber content of North American plants. Carnegie Inst. Wash. Publ. 313. 1921.
13. HOWE, T. D., Development of the embryo sac in *Grindelia squarrosa*. BOT. GAZ. 81:280-296. 1926.
14. KOCH, MINNA F., Studies on the anatomy and morphology of the composite flower. I. The corolla. Amer. Jour. Bot. 17:938-953. 1930.
15. ———, Studies in the anatomy and morphology of the composite flower. II. The corollas of the Heliantheae and Mutisieae. Amer. Jour. Bot. 17:995-1011. 1930.
16. LÖTSCHER, P. K., Über den bau und die funktion der antipoden in der Angiospermen-samenanlage. Flora 94:213-262. 1905.
17. MARTIN, G. W., Development of the flower and embryo sac in *Aster* and *Solidago*. BOT. GAZ. 17:353-358. 1892.
18. MERRELL, W. D., A contribution to the life history of *Silphium*. BOT. GAZ. 29:99-133. 1900.
19. OPPERMAN, MARIE, A contribution to the life history of *Aster*. BOT. GAZ. 37:353-363. 1904.
20. PODDUBNAJA-ARNOLDI, W., Spermatogenesis bei einigen Compositen. Planta 4:284-298. 1927.
21. SCHNARF, KARL, Vergleichende embryologie der Angiospermen. Gebruder Bornträger. 1931.
22. SMALL, JAMES, Origin and development of the Compositae. 1919.
23. WARMKE, H. E., Macrosporogenesis, fertilization, and early embryology of *Taraxacum kok-saghyz*. Bull. Torr. Bot. Club 70:164-174. 1943.
24. WILSON, C. L., and JUST, THEODOR, The morphology of the flower. Bot. Rev. 5:97-132. 1939.

